

Maternal Corn Environment Influences Wild-PROSO Millet (*Panicum miliaceum*) Seed Characteristics

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Modification of the cropping environment to make weed seed more susceptible to fatal germination or decay processes is based, in part, on the premise that seed longevity is affected by the crop-influenced environment in which seed is produced, hereafter, called the *maternal crop environment*. The objective of this investigation was to determine the influence of maternal crop environment on wild-proso millet seed production, germinability, and seed coat tone (i.e., lightness), a trait previously associated with seed longevity in wild-proso millet. Maternal corn environments were established by growing wild-proso millet plants in four morphologically different sweet corn hybrids in four replicates over 2 yr. Wild-proso millet seed was collected at sweet corn harvest, enumerated, characterized for seed coat tone, and tested for germination. Principal component factor analysis reduced six sweet corn traits measured between silking and harvest into a single maternal corn environment factor that accounted for 84% of the variation among crop canopies. Functional relationships between maternal corn environment factor scores and wild-proso millet seed characteristics were clarified by fitting linear models. For each unit decrease in maternal environment factor score, wild-proso millet seed production increased 1,535 seed m⁻², germination increased 2.2%, and seed coat tone was 1.8% lighter. These results show the size and germinability of wild-proso millet seed was highest in less-competitive maternal corn environments characterized by a short time to crop maturity and a small crop-canopy size.

Nomenclature: Wild-proso millet, *Panicum miliaceum* L., PANMI; sweet corn, *Zea mays* L.

Key words: Competition, dormancy, germinability, seed color, seed persistence, seed bank, seed production.

Control of wild-proso millet is difficult because of prolonged patterns of seedling emergence, rapid vegetative growth, tolerance to several herbicides, and prolific seed production (Bough and Cavers 1987). In a survey of sweet corn fields at harvest in the midwestern United States, wild-proso millet was among the most prevalent weed species, occurring in 47% of fields at an average density of 20,000 plants ha⁻¹ (Williams et al. 2008c). This survey also found that, at the time of sweet corn harvest, wild-proso millet produced viable seed in most fields. Moreover, crop yield-loss models project significant reductions in sweet corn yield at reported wild-proso millet densities (Williams et al. 2008b), and annual seed inputs increase wild-proso millet seedling recruitment and interference potential in subsequent crops (Cavers et al. 1992; Davis and Williams 2007).

Corresponding differences in seed germinability, soil seed-bank longevity, and coat color can be found among biotypes of wild and domesticated proso millet. Biotypes with seed lighter in color germinate more readily than biotypes with seed darker in color (Bough et al. 1986), and biotypes with olive-green to dark-brown seed persist in the soil seed bank longer than biotypes with lighter-colored seed (Bough et al. 1986; Cavers et al. 1992). Covariance in seed germinability and seed color has yet to be studied, to our knowledge, within a single wild-proso millet biotype, but in general, seed-to-seed variability in physiology and morphology within biotypes are consequences of differences in maternal genetics, maternal environment, or interactions between maternal genetics and maternal environment (reviewed by Gutterman 2000; Roach and Wulff 1987).

Interest in finding new technologies to manage the weed seed bank has fueled research on modifying the cropping environment so that weeds not only produce fewer seeds

but also produce seeds that are more susceptible to fatal germination, predation, or decay processes (Davis and Renner 2007; Schutte et al. 2008). One aspect to this approach recognizes that weed seed traits associated with longevity are affected by the crop-influenced environment in which the weed seeds matured, hereafter, called the *maternal crop environment* (e.g., Nurse and DiTommaso 2005). Given a robust maternal crop environment effect, cropping systems could be manipulated to suppress weeds and to induce plants surviving control to produce low-quality seeds that alter seedling recruitment in favor of management. For instance, commercial sweet corn hybrids differ in their ability to suppress seed production of competing wild-proso millet (Williams et al. 2007). Does variation in sweet corn competitiveness affect other weed seed traits, such as germination? Knowledge of maternal environment factors that influence wild-proso millet seeds may aid in the development of management tactics that reduce wild-proso millet fecundity and/or deplete seed banks through post-harvest seedling recruitment and control.

In this investigation, the potential to alter wild-proso millet seed characteristics through the maternal corn environment was quantified. We hypothesized that variable maternal corn environments differentially affect wild-proso millet seed production, seed germination, and seed-coat tone, which is a measure of lightness within a hue.

Materials and Methods

Maternal Corn Environments. The four commercial hybrids, ‘ACX1413BC’ (Abbott & Cobb, Inc., Feasterville, PA), ‘Mystic’ (Del Monte USA, Rochelle, IL), ‘Quickie’ (Crookham Company, Caldwell, ID), and ‘Rocker’ (Rogers Brand Vegetable Seeds, Boise, ID), used in this work were a subset of the 23 hybrids that So et al. (2009) used to identify the principal crop canopy factors associated with crop competitive ability. Hybrids were selected to represent germplasm that varied in plant architecture developed by

DOI: 10.1614/WS-D-11-00098.1

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major seed companies. Field experiments were conducted in 2006 and 2007 near Urbana, IL, using a split-plot design with four replicates. Sweet corn hybrids were planted May 29, 2006 and May 14, 2007 on 76 cm rows in 6.1 m by 9.2 m main plots. Subplots, assigned either the presence or the absence of wild-proso millet, measured 3.0 m by 9.2 m. Subplots with wild-proso millet were used to characterize weed response, whereas subplots without wild-proso millet were used to characterize aspects of the maternal corn environment (e.g., crop height, vegetative period, and canopy density). Fields had no history of wild-proso millet. Therefore, wild-proso millet seed were shallowly planted to appropriate subplots the day of sweet corn planting, resulting in mean population densities 3 wk after emergence of 72 and 126 plants m^{-2} in 2006 and 2007, respectively. Wild-proso millet seed for planting were collected the previous year from plants occurring in discrete patches in a local corn field and stored air-dry at room temperature. Seeds were planted within 8 mo of collection. Following emergence, the crop was hand-thinned to 5 plants m^{-1} of row and irrigated as needed to avoid drought conditions. Herbicides (S-metolachlor and bentazon applied after wild-proso millet emergence), interrow cultivation, and hand-weeding were used to keep the study free of weeds other than wild-proso millet.

After all hybrids had silked, crop height to uppermost leaf, oven-dry crop biomass of 2 plants $plot^{-1}$, crop leaf area index (LAI), and intercepted photosynthetically active radiation (IPAR) were recorded in weed-free plots. Two plants were harvested from the center rows, leaves were separated, and green leaf area was measured using an area meter (LI-3100C area meter, LI-COR, Lincoln, NE). LAI was estimated as the product of mean leaf area per plant and number of plants per square meter. Quantity of IPAR was measured under full-sun conditions at three locations within each plot using a linear ceptometer (AccuPAR model LP-80, Decagon Devices, Inc., Pullman, WA). At each location, two measurements of light were taken: one measurement above the crop canopy followed by one at the soil surface with the sensor perpendicular to, and centered over, one of the middle rows. All measurements were taken between 10 A.M. and 2 P.M. to minimize the influence of solar zenith angle on IPAR. IPAR was estimated as unity minus the fraction of the soil-surface to above-canopy measurements and then averaged for each plot. Growing degree days were determined using minimum and maximum air temperatures from a weather station located < 1 km from the field plots. A base temperature of 10 C was used as the minimum temperature for corn growth. The time of crop emergence was used as the reference point for accumulation of growing degree days (i.e., thermal time) to silking and harvest. Wild-proso millet seed were mechanically threshed (stationary thresher, Seedburo Equipment Company, Des Plaines, IL) from plants clipped at the soil surface from two 1-m lengths of row per plot the day of sweet corn harvest. The range of harvest dates between the earliest-maturing and latest-maturing sweet corn hybrid varied by 11 and 14 days in 2006 and 2007, respectively. Immediately after harvest, each seed lot (seed in each hybrid replicate) was cleaned using an air-column separator (South Dakota Seed Blower, Seedburo Equipment Company, Des Plaines, IL), enumerated, and kept air-dry at room temperature.

Germination Assays. Seed lots were tested for germinability in assays using a completely randomized design within 8 wk of

harvest. Assays were repeated both years. In each assay, four sets of 50-seed replicates per lot were incubated on distilled-water-moistened filter paper in petri dishes at 25/20 C day/night temperature regime with a 12-h photoperiod. Germinated seedlings were counted and removed daily for 7 d. No additional germination was observed the following week, and assays were terminated.

Seed Coat Color. Four subsamples of wild-proso millet seeds from each seed lot were scanned with a flat-bed scanner (ScanJet 5370C, Hewlett Packard, Palo Alto, CA). Seed were arranged so that the image did not include void space and so the image consisted entirely of seed. This was accomplished by standing on end a 10-cm-diam, paper tube on the scanner glass, pouring seed into the tube to a height of 1.5 cm, and scanning the bottom side of the seed column. Seed images were standardized to 30 mm by 60 mm, at 177 pixels by 354 pixels, and were characterized using the red-green-blue (RGB) color model with 255 channels per color. Specifically, the ImageJ software program (Rasband 2010) was used to determine the pixel frequency of each RGB channel within seed images. The mode of each RGB channel was identified, and color channel modes were averaged across batch subsamples. A composite seed coat tone (i.e., lightness) of each image was calculated by summing the modes of RGB scores. If all colors are at their maximum (i.e., 255, 255, 255), the resulting tone is white, whereas the tone is black when all RGB scores are zero.

Statistical Analyses. The purpose of using different hybrids in this study was to facilitate the creation of variable maternal corn environments and relate parameters describing those environments to wild-proso millet responses. However, covariance relationships are known to exist among the crop traits measured in this work. Among 23 sweet corn hybrids, crop height, biomass, LAI, IPAR, and thermal time to silking and harvest were positively correlated, with Pearson correlation coefficients ranging from 0.38 to 0.75 (So et al. 2009). Therefore, a principal component factor analysis was used to reduce the phenomorphologic crop traits measured in this study into a smaller number of factors describing variation in the crop. The principal component factor analysis was conducted across years, hybrids, and replicates, and factors were retained using Cattell's scree plot test (Johnson 1998).

A benefit of principal component factor analysis is that factor scores can be used in further analyses, such as quantifying relationships between principal factors and weed response. Therefore, wild-proso millet seed production, germination, and seed coat tone were fitted to a linear model as functions of principal factor scores using least-squares regression. In addition, the association between seed coat tone and germinability was quantified using Pearson correlation analysis. All analyses were performed in SYSTAT software (version 11.0, Systat Software, Inc., Chicago, IL).

Results and Discussion

Principal component factor analysis reduced the six crop traits into a single factor that accounted for 84% of the variation among crop height, biomass, LAI, IPAR, and thermal times to silking and harvest. Factor loadings ranged from a low of 0.838 for crop biomass, to a high of 0.963 for thermal time to silking. Relations between factor scores and

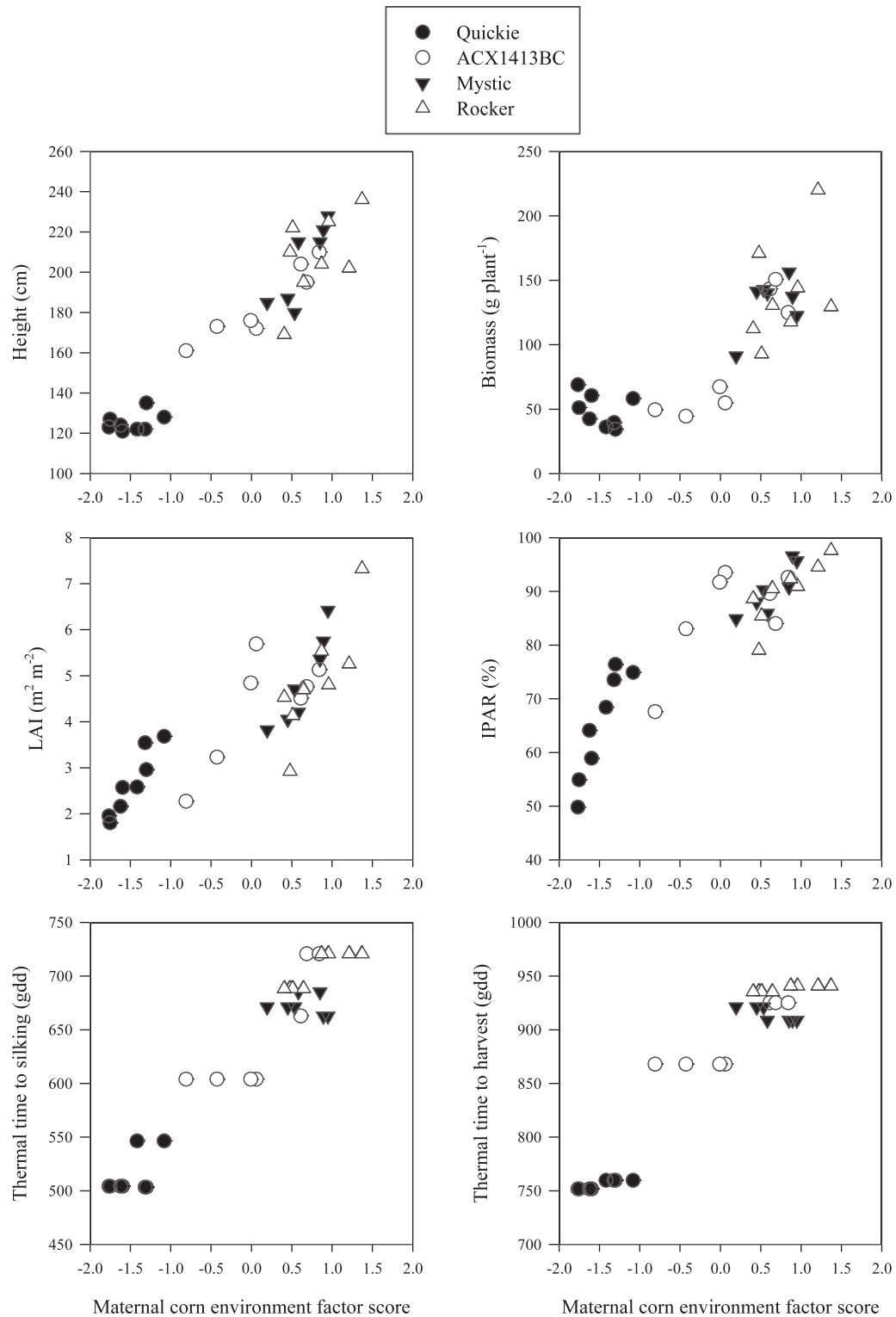
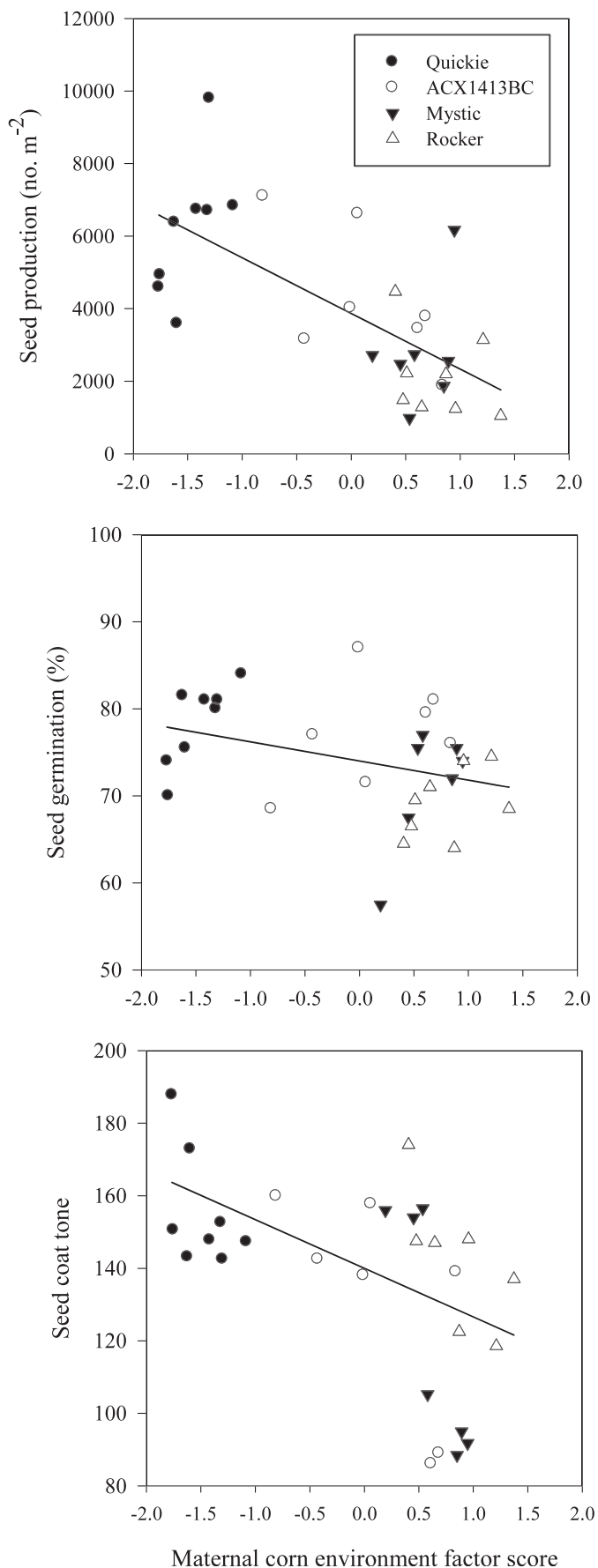


Figure 1. Relationships between maternal corn environment factor score and traits of four hybrids used in field studies at Urbana, IL. Maternal corn environment is the first principal component of a factor analysis, accounting for 84% of cumulative variance of sweet corn height, biomass, leaf area index (LAI), intercepted photosynthetically active radiation (IPAR), and thermal times from emergence to silking and harvest.

each trait revealed that the higher factor scores (e.g., scores > 0) described a crop that was taller, with a larger canopy, and longer period of phenologic development compared with lower factor scores (Figure 1). Because this factor describes a corn canopy during wild-proso millet seed development (i.e., from anthesis to seed dispersal), the factor was interpreted as

the maternal corn environment factor. This same maternal corn environment factor has been reported previously. Among 18 phenomorphologic traits, So et al. (2009) showed that sweet corn height, biomass, LAI, IPAR, and thermal times to silking and harvest loaded highly into the first factor of a principal component factor analysis.



Maternal corn environment had a major effect on wild-proso millet seed production. Each unit decrease in the maternal corn environment factor resulted in an increase of 1,535 seed m⁻² (Figure 2). Therefore, seed production was highest in maternal corn environments characterized by shorter time to crop maturity and smaller crop canopy size. Previous research also has shown that weed seed production was highest in early maturing sweet corn hybrids, relative to late-maturing hybrids (Williams et al. 2007, So et al. 2009). Despite a longer period for weed growth and reproduction in later-maturing hybrids, they are better equipped to compete for limited resources and suppress wild-proso millet fecundity.

As hypothesized, variable maternal corn environments also differentially affected the germination of seed from competing wild-proso millet plants. A negative slope coefficient between maternal corn environment factor scores and germinability indicated that for each unit decrease in maternal corn environment factor, wild-proso millet germination increased 2.2% (Figure 2). Like fecundity, germinability of wild-proso millet seed after sweet corn harvest was highest in maternal corn environments characterized by a shorter time to crop maturity and a smaller crop canopy size.

Relationships between competitive stress in the maternal environment and seed germination have been reported recently in other species. Velvetleaf (*Abutilon theophrasti* Medik.) seed that matured in competition with corn had smaller seed coats and were more germinable than velvetleaf seed that matured in velvetleaf monoculture (Nurse and DiTommaso 2005). Competition for limited resources in the maternal environment was believed to have released the seed from coat-imposed dormancy by compromising the seed coat's ability to prevent imbibition. The maternal environment also can influence embryo dormancy, which describes dormancy maintained through a physiologic condition of the embryo (Bewley 1997). One way in which maternal environment affects the level of physiologic dormancy occurs through the light environment. For example, lower germination for Powell amaranth (*Amaranthus powellii* S. Wats.) seeds maturing in competitive environments was attributed to maternal plant exposure to reduced red : far-red ratio (Brainard et al. 2005). This germination response to the maternal light occurs in many species requiring light for germination (reviewed by Gutterman 2000). For some warm-season grasses, seed dormancy is believed to be based on a combination of mechanisms within both the embryo and seed coat (Adkins et al. 2002).

Polymorphism in wild-proso millet seed-coat color across maternal corn environments varied in shades of brown, which was considerably narrower than the color range observed across proso millet biotypes that were yellow to dark brown in seed coat color (Colosi et al. 1988; Khan et al. 1997). Nonetheless, maternal corn environment had an effect on seed coat tone, with 1.8% lighter seed [i.e., 13.4/(255 × 3)] with each unit decrease in the maternal corn environment factor (Figure 1), indicating a lighter seed color in maternal corn environments characterized by shorter time to crop maturity and smaller crop canopy size. In addition, a negative correlation ($r = -0.176$, P

Figure 2. Effect of maternal corn environment factor score on wild-proso millet seed production, seed germination, and seed coat tone. Regression equations are $seed\ production = 3,868 + -1,535x$, $R^2 = 0.472$; $seed\ germination = 74.0 + -2.2x$, $R^2 = 0.053$; $seed\ coat\ tone = 140 + -13.2x$; $R^2 = 0.210$.

= 0.047) was observed between seed coat tone and germinability, suggesting lighter seed was more germinable than was darker seed within this single wild-proso millet biotype. These results are consistent with previous research that determined proso millet biotypes characterized by light (golden-yellow, grey-green) seed coats were less persistent in the soil than were biotypes with dark (black, dark-brown) seed coats (Cavers et al. 1992; Colosi et al. 1988). Khan et al. (1997) determined that proso millet biotypes with dark seed had heavier seed coats and increased resistance to imbibition damage compared with biotypes with light-colored seeds; indicating variability in seed color relates to both seed structure and capacity to withstand imbibition injury. Others have found that the physical integrity of the seed coat structures is revealed by seed coat color (Debeaujon et al. 2000; Tanska et al. 2008). Orozco-Segovia et al. (2000) determined intraspecific variability in seed coat color in the Cucurbitaceae chayotillo (*Sicyos deppei* G. Don) corresponds with differential light spectral distributions in the maternal environment.

Small, early maturing sweet corn canopies promoted the production of wild-proso millet seed that were greater in number, more germinable, and lighter in color compared with wild-proso millet seed that matured in maternal corn environments characterized by large, late-maturing crop canopies. Although phenomorphologic traits of the sweet corn canopy contribute to wild-proso millet seed response, most likely other unidentified factors are important, too. Mechanisms driving maternal environment-mediated differences in seed germinability include soil nutrients, temperature, photon flux density, photoperiod, and light spectral distribution (reviewed by: Roach and Wulff 1987; Gutterman 2000). Figueroa et al. (2010) determined that maternal temperature effects on seed germinability of common groundsel (*Senecio vulgaris* L.) can occur during flower bud development, and Mitrovic et al. (2010) found that maternal photoperiod effects on seed germinability of red goosefoot (*Chenopodium rubrum* L.) take place during the first 6 d of maternal plant growth. Thus, maternal environment effects on seed germinability potentially occur at any point during maternal plant growth and are species-specific. Our results, combined with the findings of previous studies, lead us to hypothesize the variable maternal crop environment may affect both the physiology of the wild-proso millet embryo, the physical structure of the seed coat, or both.

Previous research has identified practical implications of variability in commercial sweet corn hybrids to weed suppressive ability (Williams et al. 2007) and herbicide performance (Williams et al. 2008a). Results from the present work show variability in sweet corn also contributes to the maternal environment influence on wild-proso millet seed production and germinability. However, development of the crop canopy is influenced by a host of environmental conditions and biotic stresses. Conditions that favored small, early maturing canopies were associated with larger, more germinable wild-proso millet seed lots compared with wild-proso millet that matured in maternal corn environments characterized by large, late-maturing crop canopies. Analyses of demographic transitions of wild-proso millet illustrated the overriding effect of seed production in sweet corn on subsequent spring seedling recruitment and yield loss in a rotation crop (Davis and Williams 2007).

Limiting weed seed production by controlling plants within the crop continues to be a focal point of weed management in

field crops. Use of commercially available cultivars that offer enhanced weed suppression, although far from a new concept, could offer an immediate, meaningful contribution to weed management in sweet corn. Nonetheless, plants escaping control and producing seed remain common. That the maternal corn environment influences germinability of wild-proso millet may lead to development of new approaches to manage the weed. Perhaps action shortly after sweet corn harvest could be used to facilitate greater seedling recruitment and seed bank depletion before the onset of cold conditions that induce secondary seed dormancy. However, the type and intensity of such tactics, as well as their contribution to integrated weed management, have yet to be identified.

Acknowledgments

The authors appreciate the technical assistance of Jim Moody and comments of Adam Davis. We thank Abbot & Cobb, Crockham Company, Del Monte, and Rogers Brands for providing sweet corn seed. Mention of a trademark, proprietary product, or vendor does not constitute a guarantee or warranty of the product by the U.S. Department of Agriculture and does not imply its approval to the exclusion of other products or vendors that also may be suitable.

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Received June 14, 2011, and approved September 9, 2011.